

INHERITANCE OF FRUIT SHAPE IN CUCURBITA PEPO. I

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(WITH THREE FIGURES)

During the past few years much progress has been made in our knowledge of the inheritance of quantitative characters. We know much less, however, about the factors which control the interrelationships between these various size characters, and which thus determine the shape of the organism. The present paper is a preliminary report on some investigations dealing with certain phases of shape inheritance in the summer squash.

For the past six seasons the writer has been carrying on some breeding work with a number of the common types of *Cucurbita Pepo*. Commercial material of this species is apt to be very much hybridized and consequently to yield a remarkable variety of forms. Many strains are also self-sterile, or become so after a year or two of inbreeding. A considerable variety of types was obtained from four leading seed firms in the spring of 1916, and an attempt was made, by persistent self-fertilization, to establish from this highly heterozygous material types which would be essentially pure. Of course the majority of plants refused to set seed under these conditions, but about twenty-five were found which were self-fertile, and the offspring of these (except for a number of lines which have since been lost through sterility) have been continuously inbred for six generations. In most cases sterility disappeared by the fourth generation, and by this time such a high degree of uniformity was shown in all plant characters as to make it clear that a fairly close approach to homozygosity had been attained. In 1919 a number of crosses involving all the more notable character differences were made among these various pure types, and the uniformity of the F_1 in every case gave further assurance that the parent types were approximately pure. An F_2 generation from each of these crosses was made during the past season (1921).

A number of the pedigrees involved rather radical shape differences in the original types crossed. Several pure strains of the ordinary "scallop" or "pattypan" type were obtained (fig. 1) with fruit essentially disclike in shape, being from two to four times as broad as thick, with the teeth or scallops around the edge varying in number, shape, and development. In one race of white discs there appeared very early several plants in which the fruit differed markedly from that of the disc parent, being nearly spherical in shape, approximately as thick as broad, and with a rather weak development of teeth. Intermediate forms did not appear, and the spheres when inbred never produced any other shape. Several pure lines with spherical fruits were thus obtained (fig. 1).

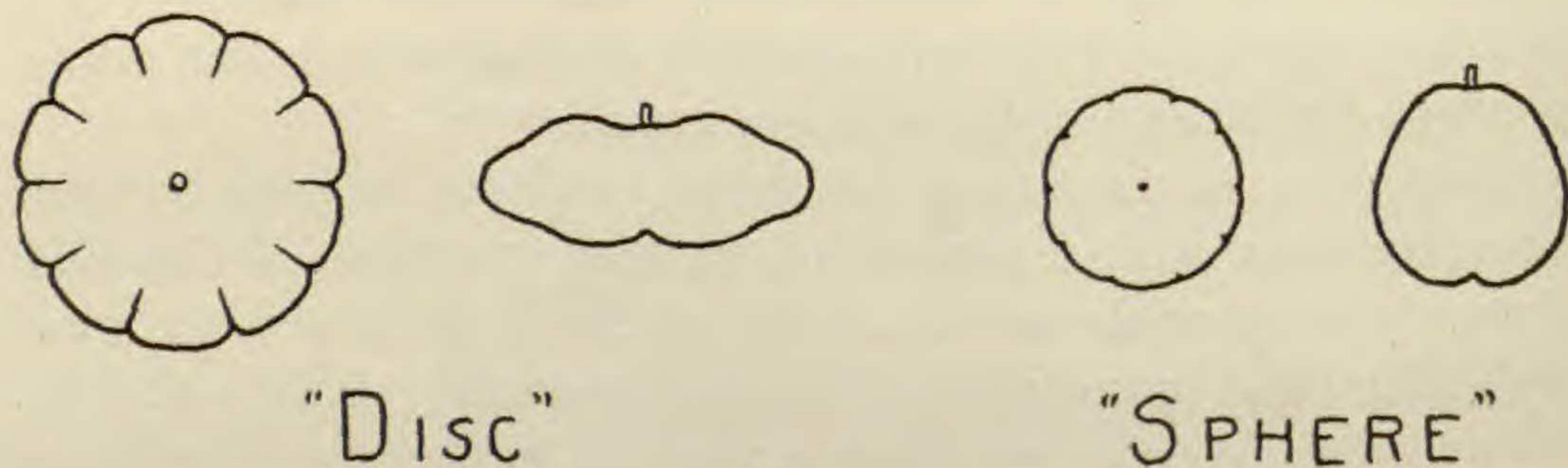


FIG. 1

A single plant of one of these spherical-fruited lines was crossed in 1919 with a plant from each of three disc-fruited lines. These three lines differed somewhat in fruit shape, one having a relatively flat disc and the others relatively deep ones, one being somewhat flatter than the other. The F_1 generation in each case showed complete dominance of the disc shape, and the type of disc (deep or flat) was essentially like that of the particular disc parent used. In the F_2 generation there was a sharp segregation into approximately three-quarters disc and one-quarter sphere. It is evident that the chief difference between these two shapes is caused by a single factor, and that this shows complete dominance. F_2 counts for the three pedigrees, together with the results expected on the single factor hypothesis, are shown in table I.

The problem is not quite so simple as this, however, for the F_2 segregates do not resemble exactly the original types, it being especially noticeable that the sphere segregates differ in shape, those

coming from the crosses where the flattest disc was used being noticeably flatter than those coming from the crosses where the thickest disc was used.

TABLE I
FRUIT SHAPE IN F_2 OF THREE CROSSES OF DISC \times SPHERE

Pedigree	Disc	Sphere
15.....	83	18
1.....	79	29
19.....	41	13
Total.....	203	60
Expectation, 3:1.....	197	66

To bring out more clearly the various shape differences, a study of the relative sizes of the two major dimensions, width and length, as represented by an index, is useful. This shape index for a given fruit is its width (the dimension at right angles to the fruit axis) divided by its length or thickness (dimension parallel to the fruit axis). The means for the shape index of parents, the F_1 , and the two extracted types in the F_2 for the three pedigrees, are set forth in table II. The frequency distribution of the individuals in the three pedigrees with respect to this shape index is also given in fig. 2.

TABLE II

MEANS FOR FRUIT SHAPE INDEX (WIDTH \div LENGTH) IN THE FOUR PURE LINES STUDIED, IN F_1 AND THE TWO TYPES SEGREGATING IN F_2 , FOR THE THREE PEDIGREES; FIGURES IN PARENTHESES ARE INDICES EXPECTED ON BASIS OF TWO-FACTOR HYPOTHESIS

PURE LINES	OBSER- VATION	EXPEC- TATION	F_1	OBSER- VATION	EXPEC- TATION	F_2	DISC		SPHERE	
							Obser- vation	Expec- tation	Obser- vation	Expec- tation
103 (sphere)	0.97								
15 (disc)....	2.48	(2.47)	15...	2.59	(2.47)	15...	2.51	(2.47)	0.86	(0.97)
1 (disc)....	2.50	(2.72)	1...	2.91	(2.72)	1...	2.61	(2.66)	1.20	(1.16)
19 (disc)....	3.28	(3.22)	19...	3.34	(3.22)	19...	2.94	(3.03)	1.50	(1.53)

Records for a comparatively small number of individuals of the four pure types are here presented, since only a few plants are grown of each of the various pure lines in any one year. The F_1 generations were also small, but the F_2 generations were considerably larger. Cultures involving much greater numbers are now being grown.

From a study of these few individuals, however, certain points stand out clearly. The F_1 shows complete dominance of the disc shape. In fact, in every case the F_1 is even a little flatter than the parent disc. This is notably the case in pedigree 1, but there is reason to believe that the pure type of this line is probably a little flatter than is shown by the individuals here portrayed.

In pedigree 15, which involves the deepest disc, both the sphere and disc F_2 segregates are essentially like the original types, being a little deeper in each case. A single factor difference between disc and sphere is apparently sufficient to account for these facts. It will be noted that there is a very sharp segregation between the two shapes in the F_2 . In pedigree 19, however, which involves the flattest disc, the F_2 spheres are decidedly flatter than the parent sphere type (1.50 as compared with 0.97), and the F_2 discs distinctly deeper than the parent disc type (2.94 as compared with 3.28). Pedigree 1 is somewhat intermediate between these, the F_2 spheres being somewhat flatter than the original sphere type, and the F_2 discs being about the same as the original disc type, but considerably deeper than the F_1 discs.

In pedigrees 19 and 1 there is evidently something more than a single disc or "flattening" factor at work. This coincident flattening of the spheres and deepening of the discs may readily be explained by assuming that there is a second dominant flattening factor, considerably weaker in its effect than the major one already discussed, and segregating independently of it. The parent disc type would possess both of these and the parent sphere type lack them both. The major difference between disc and sphere would still be caused by the larger factor, the "spheres" lacking it and the "discs" possessing it. In the F_2 , however, three-quarters of the spheres would possess the smaller flattening factor, and the average shape of the whole sphere group would thus be flatter than that of the pure type; and a quarter of the discs would lack this smaller factor and thus be less flat than the original discs in which both flattening factors are present. This would tend to bring the two shape types somewhat nearer together in the F_2 than in the pure types, a condition which evidently obtains in these two pedigrees.

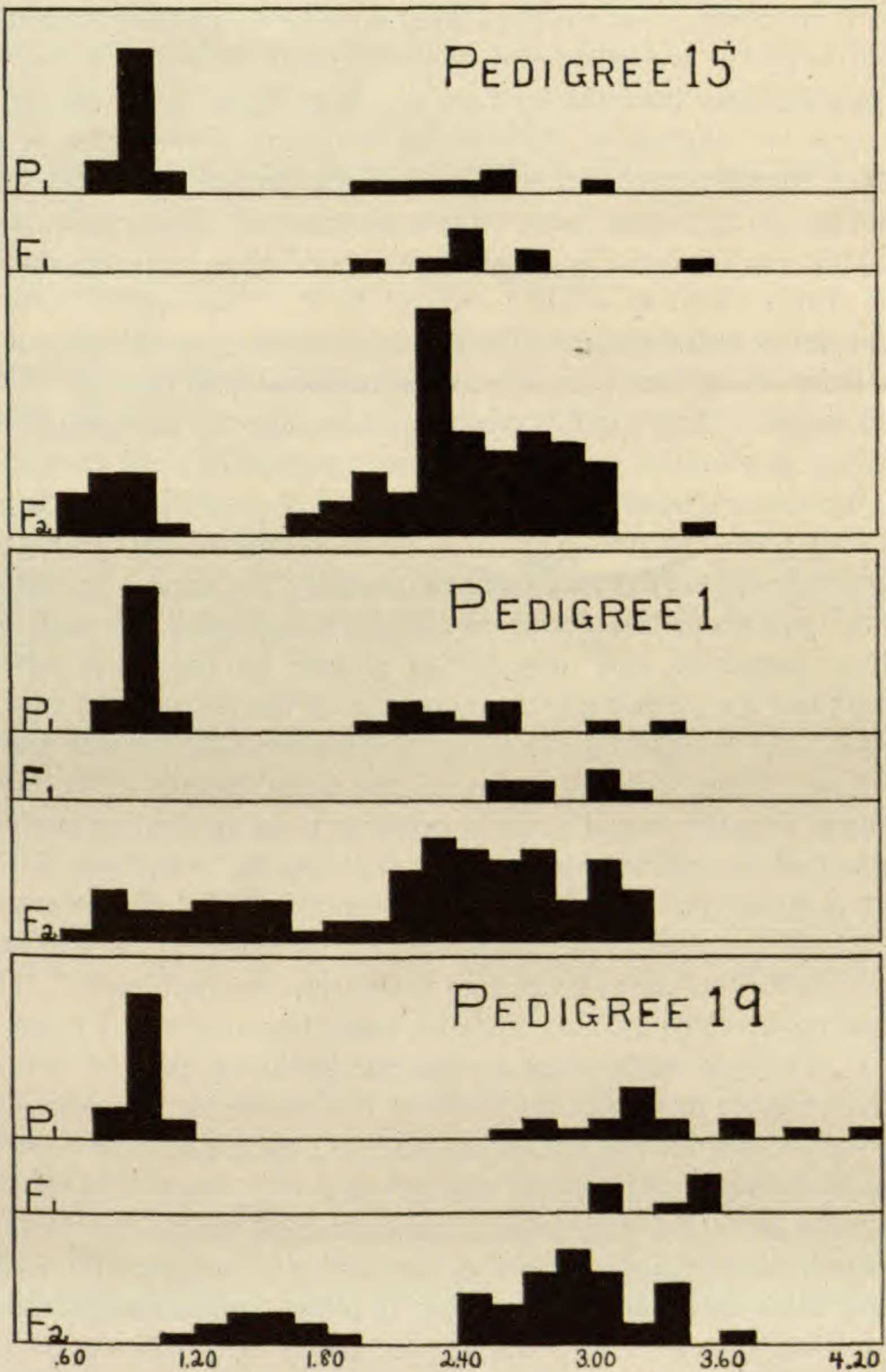


FIG. 2.—Fruit shape index (width/length) in parents, F_1 and F_2 of three pedigrees

If we assume that the discs used in pedigree 15 differ from the spheres by the possession of a single dominant flattening factor A , which increases the index by 1.50, that in pedigree 19 the disc type possesses in addition to this a second dominant flattening factor B , which increases the index by 0.75, and that in pedigree 1 the supplementary flattening factor (which we may call C) is smaller and can increase the index by only 0.25, we would obtain approximately the shapes which we actually find in the F_2 . The original sphere type has an index of 0.97. The disc in pedigree 15 would thus have an index of 0.97 plus 1.50, or 2.47, as compared with the 2.48 which was found. The F_1 and F_2 types would be expected to repeat these indices, a condition which they come reasonably close to doing. In pedigree 19, however, the parent disc (AB) would have an index of 0.97 plus 1.50 plus 0.75, or 3.22, as compared with the 3.28 observed. The F_1 should be approximately the same. In the F_2 three-quarters of the spheres would be aB , 0.97 plus 0.75, and the other quarter ab , 0.97 only, giving a mean for the whole sphere group of 1.53. Similarly, three-quarters of the discs would be AB or 3.22, and one-quarter Ab or 2.47, giving a mean for the disc group of 3.03. These indices are close to the actual figures. The same general situation would occur in pedigree 1, factor C being present instead of A , and the original disc type being AC . In table II the actual indices and the theoretical expectations are both presented.

It will be noted that this hypothesis does not explain the fact that the F_1 discs are in every case flatter than the pure types. The numbers involved are also much too small to prove such a hypothesis. They certainly seem to indicate, however, that in two of the disc types more than one factor is responsible for the shape difference between it and the sphere, and that these two factors are of unequal effect.

This is probably a rather simple case of shape inheritance. Indeed, other pedigrees at present in process of completion indicate that shape inheritance in squashes is often much more complex, involving a considerable number of factors, some of which also show lack of dominance. In GROTH'S¹ work with tomatoes, a

¹ GROTH, B. H. A., Some results in size inheritance. N.J. Agric. Exp. Sta. Bull. 278. pp. 92. pls. 34. 1915.

study of the F_2 in a number of crosses involving differences in fruit shape shows that a distinct bimodal curve is present, thus suggesting a segregation something like that here reported in squashes. In many other shape crosses studied by this investigator, however, the F_2 showed a wide range of shapes with no clear cut segregation of

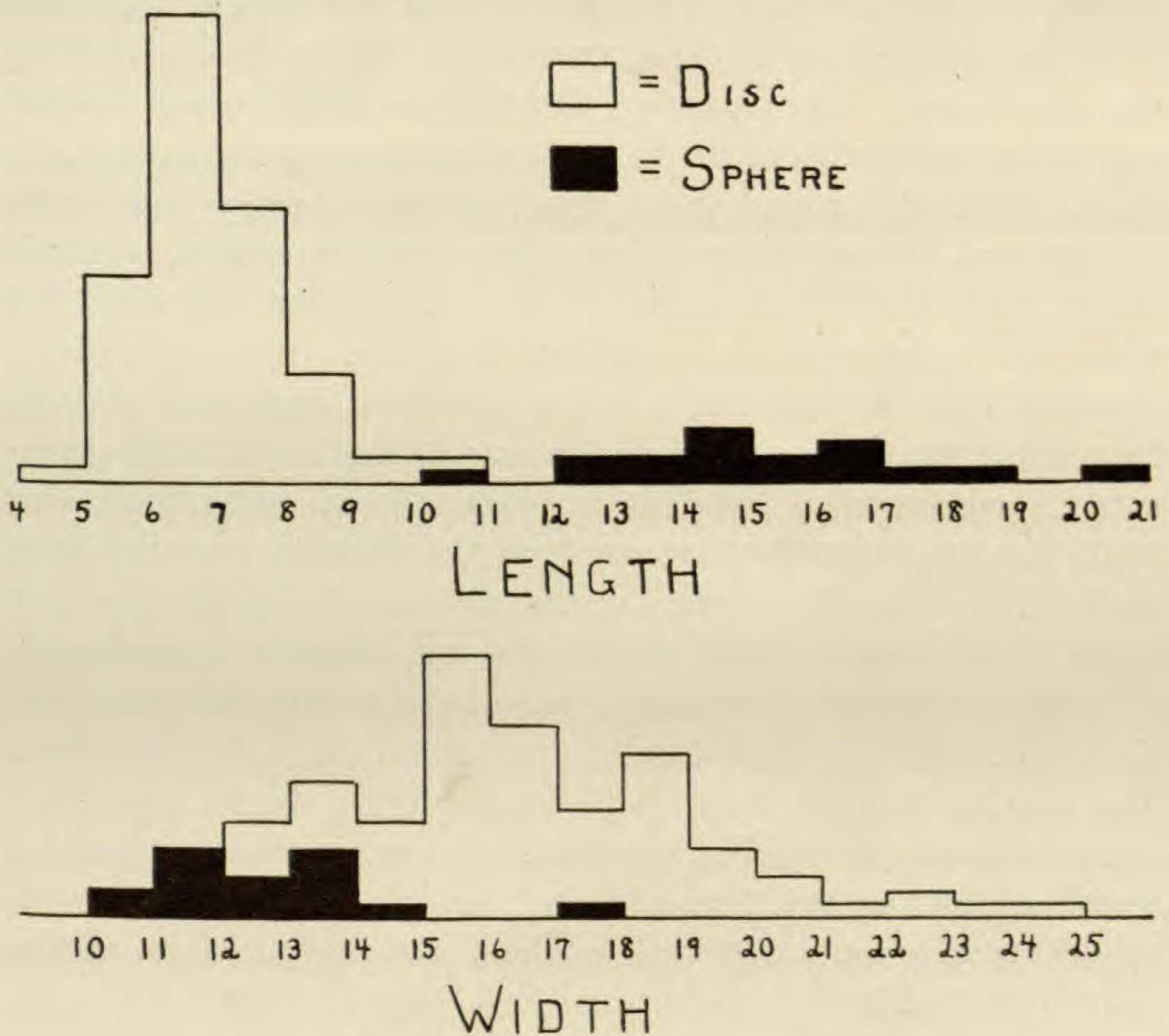


FIG. 3.—Length and width of F_2 fruits, pedigree 19

types, thus suggesting the operation of a larger number of factors. EMERSON'S² work with squashes also shows a great increase in the variability of shape in the F_2 and (apparently) no clear cut segregation. The parental types used by EMERSON, however, were not inbred homozygous strains.

It is assumed that in the present case such things as "shape factors" exist in the germ plasm and are operative. It may be objected

² EMERSON, R. A., The inheritance of sizes and shapes in plants. Amer. Nat., 44:739-746. 1910.

that the results are due merely to a segregation of those size factors which control fruit thickness and fruit width. That such an explanation is scarcely tenable, however, is indicated by a study of the actual dimensions in the F_2 , for here we find that the squashes which are the longest (thickest) are also those which are narrowest (thus producing the sphere types), and that the squashes which are thinnest are also those which are widest (thus producing the disc types). The frequency distribution of the actual lengths and the actual widths of the F_2 fruits in pedigree 19 are set forth in fig. 3. That part of each curve which consists of individuals which are spherical in shape is shaded, the discs remaining white. In fruit length there is evidently a fairly clear segregation into long and short, but no segregation is apparent in width. It is noteworthy, however, that the long fruits are not scattered irregularly through the various widths, as would be the case if length and width segregated independently, but that in practically all cases these long fruits are considerably narrower than the average, and the short fruits wider than the average, so that instead of a great variety of types in two rather vague groups, two very distinct shapes result.

There is evidently something controlling the dimensional proportions which the individual exhibits, and thus determining its shape. The relation between these shape factors and those which control size is a matter of considerable interest. The suggestion is perhaps worth considering that the ordinary "size" factors govern in some way the total amount of growth attained, and that the shape factors control the distribution and proportions of this growth.

Summary

1. Pure lines of summer squashes differing in fruit shape have been isolated.

2. In crosses between a type with approximately spherical fruits and three different races having "scallop" or "disc" fruits, the disc shape showed complete dominance in the F_1 in every case, and in the F_2 there was a sharp segregation into three-quarters disc fruits and one-quarter sphere. A single, large, dominant flattening factor thus seems to distinguish these disc types from the spherical ones.

3. In two of these crosses, the extracted spheres are distinctly flatter than the pure types, and the extracted discs distinctly deeper than the pure discs. This can be explained by assuming the operation, in each case, of a second flattening factor, also dominant, but showing a much smaller effect than the first.

4. Evidence is brought forward that shape-determining factors actually exist, and that the facts here set forth are not due merely to the segregation of size factors.

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